2008

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Morris, B. (2008) 'The effect of starvation on the size of mussels selected by the Green Shore Crab, Carcinus maenas', The Plymouth Student Scientist, 1(2), pp. 4-18.
http://hdl.handle.net/10026.1/13155

The Plymouth Student Scientist
University of Plymouth

The effect of starvation on the size of mussels selected by the Green Shore Crab, *Carcinus maenas*

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2008

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Abstract

The foraging behaviour of the green shore crabs, *Carcinus maenas*, of 24-26mm carapace width was observed over a 6 day starvation period. Edible mussels, *Mytilus edulis,* for each millimetre interval from 5-25mm were used to determine how prey size selection was effected by starvation. The most profitable mussel size for the studied crab size is approximately 9mm. At low starvation levels mussel size selection was relatively specific with the majority of selected mussels ranging in size from 7-12mm. Increased starvation caused greater variation in size selection with the majority of selected mussels ranging from 7-16mm, with a higher proportion of larger mussels being selected. After 4 days starvation random foraging behaviour and subsequent size selection was exhibited as mean mussel size values were close to the predicted random selection value of 12.5mm. Mussels were selected after progressively fewer encounters as starvation increased and consequently the maximum size of a mussel deemed profitable increased with elevated starvation. The findings are in accordance with the optimal foraging theory, since increased starvation is associated with decreasing encounter rates and low encounter rates cause broadening of a forager's diet due to the selection of successively less optimal prey.

ISSN 1754-2383 [Online]

1. Introduction

There is considerable experimental evidence that some organisms can make decisions with respect to their foraging activity, in order to achieve optimal nutritional gain from available foods. MacArthur and Pianka (1966) were the first to put forward the optimal foraging theory, which states that an organism shows preference towards a prey item which provides a high profitability. The profitability of a food item is determined by **E/h** (where **E**= calorific value of the prey item, **h**= handling time). Therefore an organism which displays optimal foraging behaviour would forage for a highly profitable food source which is of high calorific value and requires little handling time. It is suggested that upon encountering a new prey item, an optimal foraging organism will assess whether the new prey is more than or equally as profitable in terms of calorific value and handling time as the average profitability of an item which is already included in its diet (i.e. $\mathbf{E}_{new}/\mathbf{h}_{new} \geq \mathbf{E}_{average}/\mathbf{h}_{average}$). Furthermore it is suggested by the MacArthur and Pianka (1966) that optimal foraging is influenced by prey abundance. When food is abundant a foraging organism's diet is specific as the consumer can afford to reject inferior prey since there is a high probability of encountering a more profitable prey item in the time it would take to capture and handle the previous one. Conversely when prey is scarce diets are broadened as there is a low probability of encountering an optimal prey type.

Optimal foraging is thought to have evolved from an organism's innate necessity to maximise fitness and subsequent reproductive success (Stephens and Krebs 1986). The utilisation of a food source which provides all dietary requirements for minimal exertion would allow an organism to expend less energy on foraging activities and more energy on reproduction. The fundamental principle for maximising fitness is the survival of reproductively viable offspring (Darwin 1859). Therefore if a greater rate of energy gain allows for greater reproductive success then optimal foraging is beneficial in maximising fitness.

Optimal foraging can be related to food choice i.e. foods that convey the maximum net benefit (Scheel 1992, Jones 1990, Fryxell and Lundberg 1994). For example Mascaro and Seed (2001) found that *Carcinus maenas*, showed a preference towards bivalve species which gave the greatest profitability. However optimal foraging can also be related to the size of the selected optimal prey type. Several studies have investigated the effect of prey size on foraging behaviour. Werner and Hall (1974) studied prey size selection in bluegill sunfish and found that when daphnia were abundant only smaller individuals were selected, as prey abundance decreased larger individuals were

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selected in addition to the smaller organisms. Similarly Juanes and Conover (1994) found that when given a choice, blue fish consumed primarily small silverside fish due to the low handling times and high attack success rates. When small prey items became less abundant it was found that larger sub-optimal sized silverside fish were incorporated into their diet in addition to the more optimal small sized prey. An apparent conformity in the aforementioned studies is clear. When a prey species is abundant, smaller more profitable individuals are selected and larger individuals are rejected. As prey abundance decreases larger individuals are included in the diet, even though they may be less profitable. This concurs with a prediction from optimal foraging theory which states that a predator should reject less profitable prey items from its diet at higher densities of profitable prey (MacArthur and Pianka 1966, Bence and Murdoch 1986).

Molluscivore crabs have been at the forefront of studies testing the optimal foraging theory in relation to prey size selection (Elner and Hughes 1978, Hughes 1979, Hughes and Elner 1979, Hughes and Seed 1981, Blundon and Kennedy 1982, Arnold 1984). It has been shown that, in marine systems, the pattern of preference for small-sized molluscan prey is wide spread among decapod crustacean predators (Micheli 1995, Juanes 1992). Elner and Hughes (1978) observed that under unlimited prey conditions crabs chose mussels of a small to intermediate size, close to the predicted optimum. This occurred after a brief period of manipulation which suggested that the crabs could assess the profitability of a prey item before selection occurred (concurrent with the foraging model suggested by MacArthur and Pianka 1966). As the optimum sized mussels are depleted, crabs selected prey both above and below the optimum size. A possible explanation for the reluctance of less optimal size selection is that large mussels require the expenditure of excessive amounts of energy in order to gain access to the food source and very small mussels are often mishandled by the chelae, thus increasing handling times (Rheinallt 1986). Furthermore Hughes and Seed (1981) found that the blue crab, *Callinectes sapidus*, preferred smaller mussel sizes since it simultaneously minimised handling time and maximised net gain of energy intake. This proves that time minimisation plays an important role in prey size selection. Lawton and Hughes (1985) observed similar behaviour in juvenile *Cancer pagurus* feeding on *Littorina littorea*. Smaller prey were incorporated into the diet first as they succumbed more easily to an attack, this reduced the energy requirement for penetrating the armour and consequently reduced handling time.

Prey size selection is affected by prey abundance, but can also be affected by satiation levels. A study by Hart and Gill (1992) found that only small *A. aquaticus* were consumed when

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satiation was reached in the three-spined stickleback. Thus prey choice becomes more selective as the necessity to feed decreases. Conversely as hunger levels increase prey size selection becomes less specific and larger *A. aquaticus* are consumed, despite the fact that this size of prey might not result in optimal nutritional gains. The trade offs between hunger and prey size selection is well documented in literature for many organisms (Marti and Hogue 1979, Molles and Pietruszka 1986, Bence and Murdoch 1986). In contrast, while *Carcinus maenas* has been shown to select prey in a way which maximises the energy intake in accordance with the optimal foraging theory (Elner and Hughes 1978), hunger dependent prey size selection in this species has yet to be studied.

This paper presents a study investigating the effect of starvation on size selection in the green shore crab, *Carcinus maenas*, feeding on the edible mussel, *Mytilus edulis*. The green shore crab has been chosen for this study as it has a widespread distribution in estuarine and coastal waters and because is also known to forage extensively on commercially exploited bivalves (Ropes 1968). Consequently a greater understanding of the factors which effect prey selection may help control predation in commercial prey species. Subsequent laboratory experiments were designed to ascertain whether prey size selection is affected by starvation level.

2. Methods

Carcinus maenas, of 24- 26mm carapace width were collected from The Hoe, Plymouth (Nat. Grid Ref. SX 477 539). Only male crabs were selected, identified by a narrow abdomen. *Mytilus edulis* ranging from 5-25mm in length were collected from mussel beds in Whitsand bay, Cornwall (Nat. Grid Ref. SW 362 275). Each crab was placed in a separate 15x20x15cm plastic holding aquarium, filled with aerated seawater and kept at 11ºC. Each crab was fed a single lance fish, everyday for five days to standardise starvation. Any remnants of lance fish left over from the previous day were removed before a fresh lance fish was added. The mussels were measured to the nearest mm using callipers and the length was marked on each shell using a graphite pencil. Cunningham and Hughes (1984) determined that *C. maenas* would only consume mussels up to half their size, however their experiment did not use crabs which had been starved for long periods of time, therefore mussels ranging from 5-25mm were used in the experiments.

All experiments were conducted using the same procedure. An experimental tank (30x20x15cm) was set up with aerated sea water and kept at 11ºC. Observations were recorded over 6 consecutive days, with starvation increasing with each day. At the start of each observation a Perspex

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partition was placed to the right of the aquarium to restrain the crab. Twenty one mussels were added haphazardly on the other side, one for each mm interval ranging from 5-25mm. The partition was removed and the crabs' foraging behaviour was observed. In most cases the crab would handle various mussels before one was selected. To determine whether a mussel had been selected, observations were only recorded once an attempt was made to open the mussel using the mouthparts and mandibles to chip the posterior edges of the mussels' valves (Ameyaw-Akumifi and Hughes 1987). Any foraging behaviour observed up until this point was not considered as prey selection. Two series of experiments were performed; firstly to investigate hunger dependent diet selection, secondly to look at hunger dependent diet rejection.

2.1 Hunger dependent prey selection

Twelve male crabs were used, each with a carapace width between 24-26mm. As prey selection occurred, the crab was restrained by the partition and all the mussels were removed, including the one which was selected. The selected mussel was replaced with a new mussel of an equal size to avoid any bias in subsequent experiments, caused by a weakened shell. The observations were repeated three times for all twelve crabs for 6 starvation days.

2.2 Hunger dependent prey rejection

In the previous prey selection experiment it was observed that at low starvation, it was rarely the first mussel encountered which was subsequently selected. Frequently mussels were encountered and handled without any attempt to open them. Four crabs were used in this experiment due to time and resource limitation. Rather than recording the selected mussel size, in this investigation the foraging behaviour of each crab was observed and the size of any mussel encountered and handled, before selection occurred, was recorded. This study was continued for 6 days of starvation.

Subsequent data analysis was performed using MINITAB version 15; graphs were created using the same software.

3. Results

3.1 Mussel size selection

Since triplicate observations were carried out per crab, a one way ANOVA for each starvation day was carried out to determine whether there was any significant difference in the three observations (Bartletts tests were applied in each case and no significant difference in variance was found therefore a one way ANOVA is a suitable statistical test).

Six out of seven starvation days showed no significant difference for the triplicate observations (Day 0 P=0.922, Day 1 P=0.403, Day 2 P=0.291, Day 3 P=0.404, Day 5 P=0.819, Day 6 P=0.494). Starvation day 4 did show a significant difference

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(P=0.036), however after reviewing the triplicate results for day 4 no clear trend was apparent. Furthermore since the majority of starvation days showed a vast insignificance in the triplicate data this significance can be treated as an anomaly and is due to a type 1 error. Therefore all data can be pooled for subsequent statistical analysis.

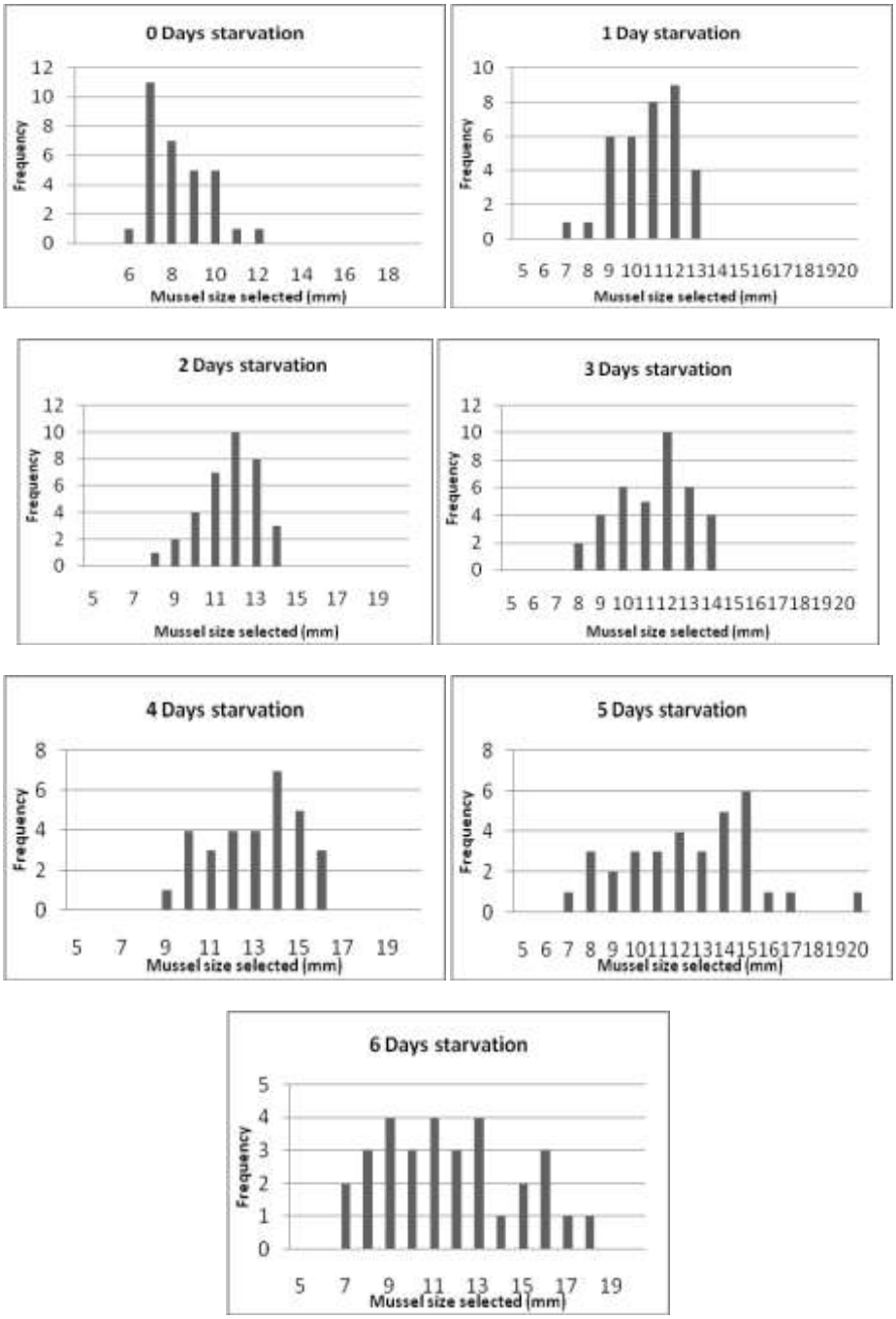

Fig. 1- Seven graphs which show the frequency of selected mussel size with increased starvation time.

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Crabs exhibited clear differences in mussel size selection with increased starvation time. There are two observed effects; firstly a change in mean mussel size and secondly a change in the variation of selected mussel size (see Fig 1). Relatively small mussels were selected at a low starvation time, with most crabs showing preference towards mussels <13mm during these periods. As starvation increases larger mussels are selected, although very large mussels (i.e. >20 mm) are always rejected. Mean median and modal sizes suggest that the size of mussels selected increases with starvation time, however extreme starvation appears to decrease the average selected mussel size (see fig 2).

A test for equal variance proved negative (Bartlett's Test P <0.001) therefore a Kruskal-Wallis test was used as an alternative to a one way analysis of variance. There is a highly significant difference in the median size of mussels selected with starvation time (Kruskal-Wallis, H=62.63, DF=6, P <0.001). The median size of selected mussels increases with starvation until day 4 where the median mussel size decreases back to the day 1 starvation value by day 6 (i.e. 11 mm).

The mean mussel size increases with starvation time until day 4 where the mean size of mussels selected begins to decrease (see fig 2). For figure 2 a quadratic model (F=8.91, DF=2 P=0.034, R-sq = 81.7) proved far more accurate in calculating a regression line than a linear model (R-sq = 56.8). A regression analysis (F= 42.59, DF= 1,241, P <0.001) showed there is a highly significant difference in the mean size of mussels selected. Mean mussel size increases with starvation until day 4 where there is an apparent reduction in size selection.

Although there appears to be a parabolic relationship in figure 2, it is likely that the curve plateaus after 4 days. At low starvation levels, mussel selection is determined by crab preference. As starvation increases mussel selection becomes more random, as preferences towards optimal prey sizes are negated by hunger mechanisms. If a crab is exhibiting random selection then the average selected mussel size would be a similar numerical value as the average size of mussels available for selection, ranging from 5-25mm (average=15mm). However mussels over 20mm were never selected, therefore the real range of mussel sizes is 5-20mm with an average of 12.5mm. At day 4 the mean size of mussels selected (12.53mm) is very close with the expected random selection size value (see fig 2), showing that this level of starvation can be associated with a random foraging behaviour. Therefore increased starvation ($\geq$ 4 days) would cause similar randomised foraging behaviour and the apparent decrease in mean mussel size can be attributed

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to the random probability of encountering small prey sizes.

At low starvation times size selection is relatively specific with a small range in selected mussel size. As starvation increases a greater proportion of larger mussels are selected and selection becomes less specific and more random therefore increasing the range of selected mussel sizes (see fig 3).

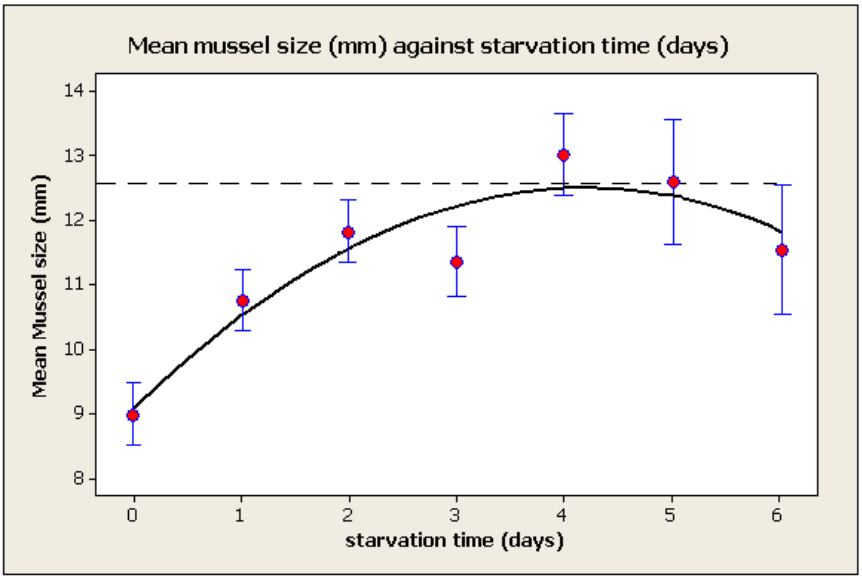

Fig. 2- The mean size of mussels selected with starvation time. Quadratic regression line (Equation- Average Mussel size (mm) = 9.797 + 1.195 Ts - 0.1387 Ts^2) (where Ts= starvation time) (R-sq = 81.7%). Confidence intervals (95%) included. Dotted line showing the mean size of mussel selected at day 4 starvation determined by the regression line (12.53mm).

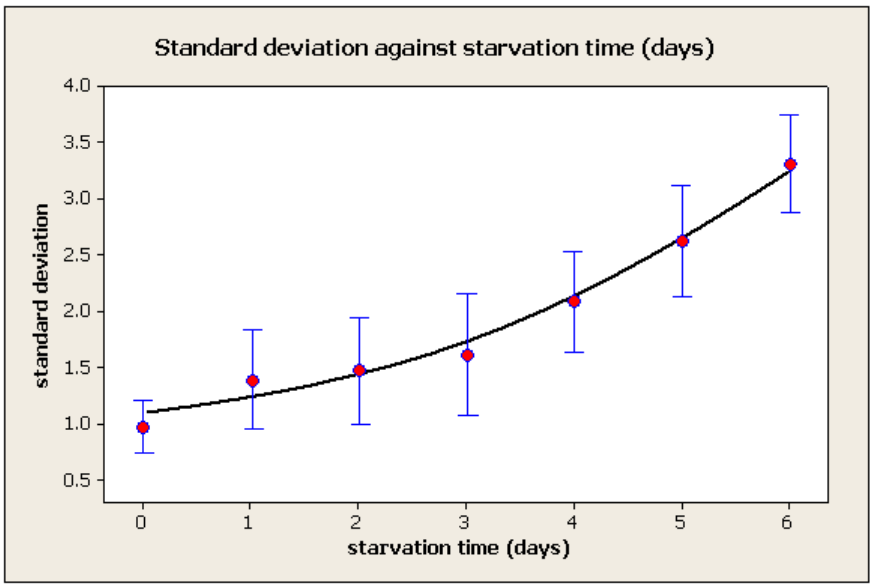

Fig. 3- The standard deviation of the mussel size selected with starvation time. Curve fitted using a quadratic model (Equation- standard deviation = 1.075 + 0.0843 Ts + 0.04629 Ts^2) which shows an exponential increase in standard deviation with starvation time. Confidence intervals included (95%)

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The standard deviation of selected mussel size increases with starvation time. For figure 3 a quadratic model (F= 40.91, DF= 2 P< 0.001 R-Sq = 98.2) proved more accurate for a fitted line plot compared with a linear model (R-Sq = 92.8). The exponential increase in standard deviation (see fig 3) shows an increase in the variation of the size of mussels selected with starvation time.

3.2 Mussel size rejected

There is a strong positive correlation between the size of rejected mussels and starvation time (see figure 4). Regression analysis (F = 38.31, DF = 1, 91, P < 0.001) shows that as starvation time increases there is a highly significant difference in mussel size rejection. At low starvation levels relatively small mussels are rejected. As starvation levels increase the mean size of rejected mussels increases since smaller mussels are subsequently selected.

Since the size of rejected mussels increases with elevated starvation it could be expected that the number of mussels which were rejected by a crab would decrease with increased starvation. This is due to progressively larger mussels being selected at elevated starvation levels which would have been rejected at lower starvation levels. As the maximum size of a mussel which could be selected increases with starvation, fewer mussels which are deemed too large for consumption will be encountered, thus decreasing the number of rejections upon encounter.

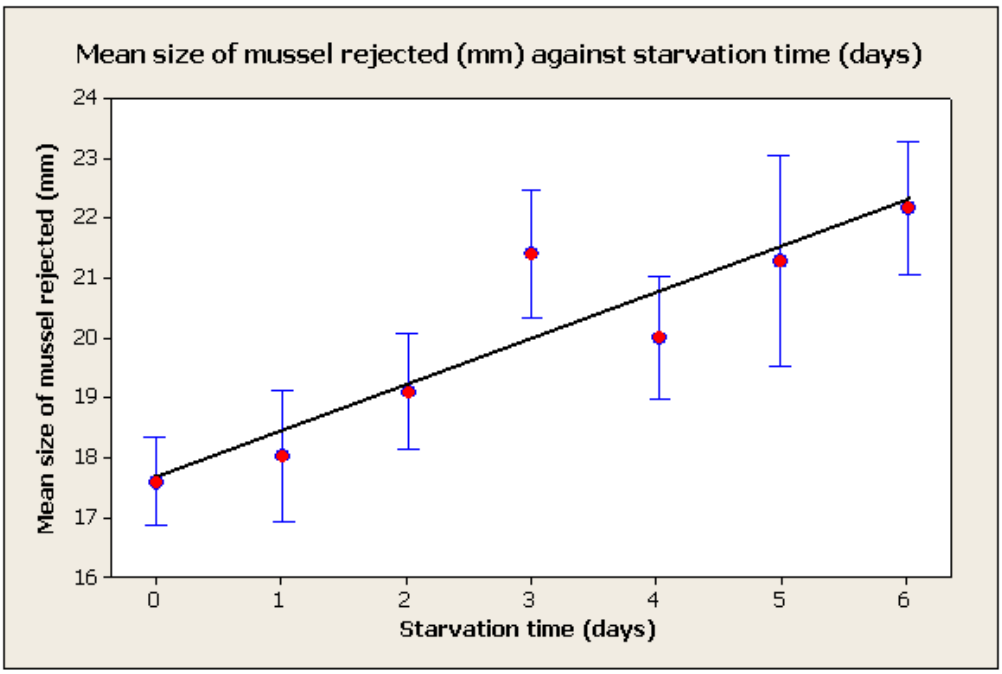

Fig. 4 – The size of mussels rejected before one is selected with increasing starvation time. Liner regression line (Equation- Size of mussels rejected = 17.55 + 0.7603 Ts) showing a positive correlation. Confidence intervals included (95%).

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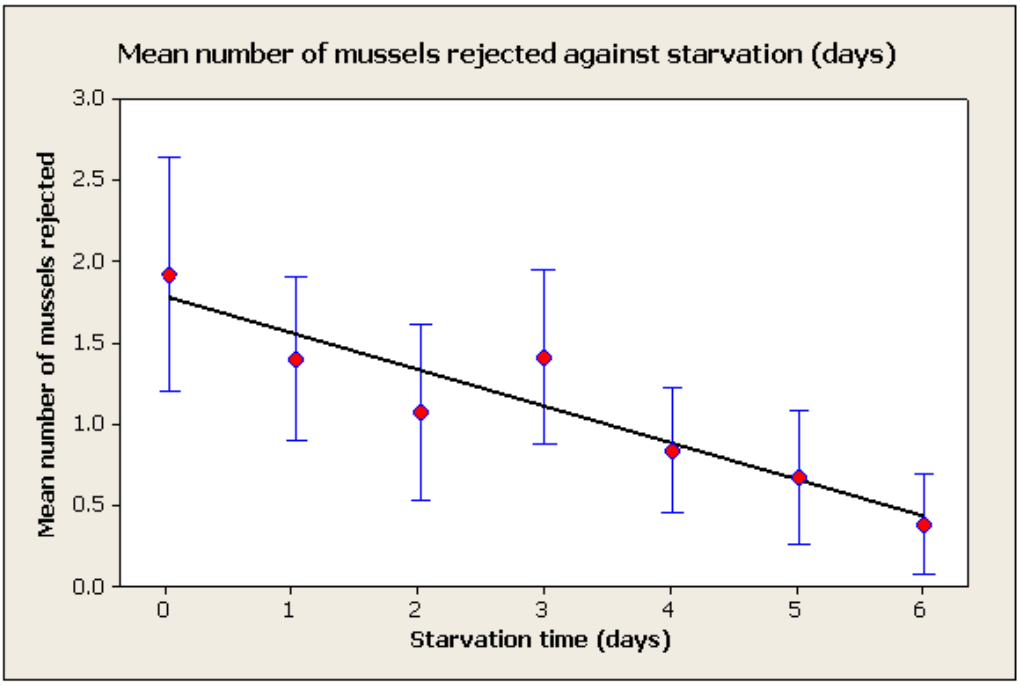

Fig. 5- The mean number of mussels rejected with increased starvation time. Linear regression line (Equation- No. of mussels rejected = 1.777 - 0.2232 Ts) showing a negative correlation. Confidence intervals included (95%)

The negative correlation between number of mussels rejected and starvation time (see fig. 5) agrees with the expected observations. Regression analysis ($F = 14.71$, $DF = 1, 82$, $P < 0.001$) shows that there is a highly significant difference between number of mussels rejected and starvation time. At low starvation levels a greater number of mussels are rejected than at high starvation levels. This confirms that selection becomes less discriminate as starvation increases

4. Discussion

Carcinus maenas foraging behaviour becomes less specific with increased starvation. At low starvation levels prey size selection is specific, with relatively small mussels being selected, since these gave the most profitable gains for the handling time required (Elner and Hughes 1978). As starvation increased selection became more random, with a proportion of larger, less profitable sizes being selected even though optimal sized mussels were still available. This behaviour has been observed in literature for many other organisms. In a study of Screech Owls, Marti and Hougue (1979) found that when starved for 36 hours a greater proportion of large mice (30-49g) were selected, although a range of sizes were selected. In comparison, satiated owls displayed specific size selection with a high proportion of small mice (10-19g) being consumed. Molles and Pietruszka (1986) observed similar foraging behaviour in

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the stonefly, *Hesperoperla pacifica*. Fasted stoneflies were found to consume a wide range of prey sizes, whereas satiated stoneflies concentrated attacks on intermediate prey.

The differences in foraging behaviour displayed by a satiated and a fasted organism can be explained by the probability of encountering optimal prey sizes. A satiated organism would have experienced foraging success, suggesting that there is an abundance of prey items in its foraging patch. Therefore there would be a high probability of subsequent encounters with optimal prey sizes, allowing the satiated organism to be selective in its foraging activities, rejecting prey types which were deemed less profitable. As hunger levels increase, an organism would have experienced a period of low/no prey abundance and therefore it can be assumed that there would be a low probability of encountering an optimal prey type. It must therefore approach foraging activity in a less specific manner, consuming organisms which would be deemed unprofitable at high satiation (MacArthur and Pianka 1966).

At low starvation *Carcinus maenas* were observed to consume relatively small mussels (7-12mm). Larger mussels (>14mm) and very small mussels (≤6mm) were rarely selected. If foraging behaviour in *C. maenas* was random at low starvation the mean selected mussel size would be similar to the average size of mussels available for selection, 12.5mm (>20mm mussels were excluded as they were never selected). However the mean selected mussel size for low starvation levels were considerably lower. This suggests that *C. maenas* assesses the profitability of a prey item before selection occurs and is concurrent with previous predictions of optimal foraging behaviour (MacArthur and Pianka 1966, Elner and Hughes 1978). As starvation increases foraging becomes increasingly random and by day 4 size selection is in accordance with predicted random prey size selection (i.e. 12.5mm). It can be assumed that if increasingly random foraging behaviour is associated with elevated starvation levels that the most profitable mussel size is selected at day 0 where satiation is at a maximum. Therefore the optimal mussel size for *C. maenas* of 24-26mm carapace width is approximately 9mm.

The increase in mean selected mussel size up until day 4 is associated with increasingly random foraging behaviour and is due to the lack of available prey species with elevated starvation. In the experiment increasing starvation times inevitably caused progressively fewer prey encounters by the crab and caused the selection of prey items larger than the predicted optimum. This is explained by the negative correlation between the number of mussels rejected and starvation time. As starvation increases a crab selects a mussel after fewer encounters and at high

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starvation levels selection generally occurred upon the first encounter regardless of size (with the exception of mussels >20mm). Random foraging occurs with elevated starvation because the assessment of the profitability of a mussel size is limited and the first mussel encountered is selected regardless of optimal size preference.

The preference towards smaller mussel sizes at low starvation can be explained by the optimal foraging theory in that a smaller mussel provides optimal nutritional gains per unit time (Schoener 1971). However Juanes (1992) suggests that size selection may be primarily due to chelae preservation. In this study it is suggested that crabs select smaller mussel sizes, since they require less force to be broken open, thus there is less risk of chelae damage. Chelae are an important asset for a crab as they are used in mating displays, defence of territory and defence from predators (Abello et al. 2004). Therefore it is suggested that the preservation of chelae is of high importance to the crab. Another explanation for the prey size selection is the consequences of a low handling time associated with small mussel sizes. Hughes and Seed (1981) suggest that predation stresses experienced by molluscivore crabs in the wild cause them to forage for smaller shelled molluscs, since handling times are greatly reduced. This allows crabs to minimise time spent foraging in an exposed environment, thus reducing the risk of predation.

While the most probable explanation for an average increase in mussel size selection with lower starvation levels (1-4 days) is that foraging behaviour becomes increasingly random, another explanation could be that mussel size selection is dependent on gut satiation. Turesson et al. (2002) determined that prey size increase was disproportional to gut satiation. The limited size of the gut, might bias selection towards small prey because satiation allows only the consumption of small but not large prey. Consequently as starvation increases more space becomes available in the gut to accommodate larger prey items.

The smallest mussels (5mm) were never selected throughout the experiments regardless of starvation time. The low handling time, due to weak shell defences, and nutritional gains would theoretically make this size class suitable for selection when starvation causes a deviation from the optimal size. One explanation for this lack of selection is the limitation of chelae dexterity (Rheinallt 1986). Large size differences between mussel and crab chelae, causes increased difficulties in prey manipulation and therefore increased handling time. An increased handling time makes the nutritional gains from such a small prey negligible, therefore very small mussels are not selected.

Similarly the largest mussels (>20mm) were never selected throughout the

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experiment regardless of starvation time. Furthermore the rejection of the largest mussels rarely occurred as handling and subsequent size assessment of large prey did not take place. This suggests that crabs use some visual cues when foraging for mussels and tactile foraging is not exclusive, this conclusion is contrary to that reached by Hughes and Seed (1995). Although crabs have the ability to access large mussels using an uneconomical boring technique (see Elner 1978), the energy requirements and long handling times for such techniques make nutritional gains negligible in comparison to the increased risk of predation.

The increase in the size of mussels rejected with starvation time is an expected observation in accordance with the optimal foraging theory. One of the main predictions of the model is that a forager should accept successively less profitably prey only when encounter and subsequent consumption rates with highly profitable prey fall below a critical level (MacArthur and Pianka 1966). When a crab experienced starvation in the experiment it encountered no prey items for a prolonged period of time. Furthermore encounter and consumption rates became increasingly scarce as starvation days increased. Therefore larger less optimal mussels are progressively selected as starvation increases.

In conclusion starvation has a profound effect on mussel size selection in the shore crab, *Carcinus maenas*. At low starvation specific foraging behaviours can be observed which result in a size selection close to the predicted optimum. As starvation increases prey encounters are greatly reduced and selection becomes less specific as resulting in the selection of less profitable mussel sizes. Mussel sizes at both extremes are never selected since increased handling times make these sizes unprofitable. Rejection of mussels is less frequent as starvation time increases as the maximum size of a mussel deemed to be profitable increases with hunger level.

Further investigations should focus on the effect of starvation on foraging times. Since this study focused primarily on prey size selection, future research should be aimed at determining whether foraging times are reduced when starvation is experienced.

Acknowledgements

With thanks to Dr. M Uttley for his advice and assistance.

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ISSN 1754-2383 [Online]